Bull. Southern California Acad. Sci.
109(1), 2010, pp. 8–14

Morphological and Anatomical Characteristics of Blackbrush (*Coleogyne ramosissima* Torr.) Leaves: A Review of Literature

Simon A. Lei

Department of Educational Psychology, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154-3003, tel: (702) 895-3953, fax: (702) 895-1658, email: leis2@unlv.nevada.edu

Abstract.—Leaves of blackbrush (*Coleogyne ramosissima* Torr.) shrubs share a number characteristics of leaves of both xerophytic and sclerophyllous shrubs. Despite some leaf surface (morphological) and anatomical similarities with typical xerophytic leaves, blackbrush leaves are more similar to typical semi-arid coastal chaparral plants in Mediterranean and southern California, or cool and high elevation inland desert perennial plants. Semi-deciduous, thick blades, well-cutinized epidermises, numerous small leaves, sclerophyllic leaves, hypostomatry, sunken stomata, thickened epidermal cell walls, and abundant abaxial and adaxial trichomes are characteristics of blackbrush plants, as well as typical woody xerophytic and sclerophyllous plants. Blackbrush also exhibit summer dormancy, with characteristics of revolute margins, uniseriate hypodermis, biseriate epidermis, bifacial palisade parenchyma, and intercellular air space in leaves; all of which are characteristics of leaves from sclerophyllous chaparral plants. Overall, xerophytic and sclerophyllous leaf designs are similar among blackbrush, warm desert plants, and semi-arid coastal chaparral plants, presumably due to many climatic and edaphic attributes shared by the inland Mojave Desert and coastal southern California. Because of a lack of consensus in current literature, morphological and anatomical characteristics of blackbrush leaves continue to be a curious dilemma to many botanists and plant ecologists.

Introduction

Blackbrush (*Coleogyne ramosissima* Torr.) is a shrub occurring at mid-elevations in the Mojave Desert. Blackbrush occur primarily along the Colorado River drainage and several adjacent enclosed basins of the Great Basin-Mojave Desert transition zone (Bowns and West 1976, Pendleton and Meyer 2004). Blackbrush leaves share some of the characteristics of xerophytic leaves that are typically small with reduced cell size, thick cuticle and blades, cylindrical, well-developed palisade mesophyll, and dense adaxial pubescence (Rundel and Gibson 1996). Such leaf design is generally interpreted as a response to arid habitats with water deficits and poor soil nutrients (Beadle 1966, Rundel and Gibson 1996). Blackbrush leaf anatomy shows features of typical of many desert species (Bowns 1973, Bowns and West 1976). However, recent morphological and anatomical investigations have revealed that blackbrush leaves do not possess typical internal xerophytic leaf design (Gibson 1996, Rundel and Gibson 1996) despite their xeromorphic appearance. Plants, having revolute leaf margins and hypostomatic leaves with hypodermis, are common in some sclerophyllous scrub (Coastal chaparral) communities of Mediterranean-type climate in southern California or cool and high elevation (semi-arid) xerophytic plant communities in warm deserts (Gibson 1996).

Table 1. A comparison among leaf morphology of blackbrush, typical woody xerophytic, and typical sclerophyllous Mediterranean (coastal) chaparral plants. The letter "X" indicates the presence of a leaf characteristic (Gibson 1996). A parenthesis around an "X" also indicates a characteristic of xerophytic or sclerophyllous plants based on the study of (Lei 1999).

Morphological traits	Blackbrush	Xerophyte	Sclerophyll
Summer dormancy	X		X
Numerous leaves	X	(X)	(X)
Evergreen or semi-evergreen	X		X
Thick blade	X	(X)	(X)
Small-sized leaves	X	(X)	(X)
Tough, leathery (rigid) leaves	X	(X)	X
Revolute leaf margin	X		X
Adaxial trichomes	X	X	X
Abaxial trichomes	X	X	X
Amphistomatry		X	X
Hypostomatry	X	(X)	X
Sunken stomata	X	(X)	X

Although the Mojave climate is an arid continental desert, it resembles Mediterranean climate with cool winters, light precipitation and warm, dry summers (Rowlands et al. 1977). The North American monsoons cause episodic thundershowers from July through September annually.

Previous research studies by Bowns (1973), Bowns and West (1976), Gibson (1996), Rundel and Gibson (1996), and Lei (1999) have increased our understanding regarding the anatomical features of blackbrush leaves. The former two research studies found that blackbrush leaf anatomy show features typical of xerophytic shrubs. In contrast, the latter three studies found that blackbrush anatomy is more typical of semi-arid coastal (Mediterranean) chaparral than arid inland desert shrubs. The current literature apparently does not agree whether blackbrush is a xerophytes or a sclerophyll. This article reviews blackbrush leaf surface (morphological) and anatomical features, and attempts to determine whether such features are more similar to xerophytic or to sclerophyllous leaves based on the data collected from previously published literature.

Morphological Characteristics

Blackbrush and chaparral plants have adapted to a summer drought and winter rain climatic pattern. Blackbrush are semi-evergreen, often experiencing summer dormancy to the extent that portions of their leaves desiccate and fall off during dry summer seasons. This phenomenon is shared by most chaparral plant species (Bakker 1984). In summer months, leaves of blackbrush and many chaparral plants are semi-evergreen, which also occurs in some xerophytic plants in order to conserve water. Summer months are typically the time of dormancy. In general, the most active growth season is from late winter through spring when soil moisture and air temperatures are optimal for growth conditions (Bakker 1984).

Leaves of blackbrush contain abundant trichomes (Table 1), especially on the abaxial surface. Dense pubescens is effective in blocking excess sunlight and in reducing water loss (Rundel and Gibson 1996). Small, thick leathery leaves of blackbrush and typical chaparral plants can greatly reduce moisture loss and are well-adapted to xeric sites. A strong correlation exists between leaf size and habitat aridity, with more xeric sites tend to support shrubs with smaller leaves (Bakker 1984).

Table 2. A comparison among leaf anatomy of blackbrush, typical woody xerophytic, and typical sclerophyllous Mediterranean (coastal) chaparral plants. The letter "X" indicates the presence of a leaf characteristic (Gibson 1996). A parenthesis around an "X" also indicates a characteristic of xerophytic or sclerophyllous plants based on the study of (Lei 1999).

Anatomical traits	Blackbrush	Xerophyte	Sclerophyll
Reduced cell size	X	(X)	(X)
Well-cutinized epidermises	X	X	X
Thickened epidermal cell wall	X	(X)	X
Uniseriate epidermis		X	
Biseriate epidermis	X		X
Hypodermis	X		X
Bifacial palisade	X		X
Isolateral palisade		X	
Intercellular air space	X		X

Blackbrush leaves exhibit sunken stomata that are evident early in leaf development, but become more prominent as the leaf matures (Bowns 1973, Bowns and West 1976). Blackbrush leaves are hypostomatic (Table 1), implying that stomates are located on the abaxial epidermis only. Stomates are connected to large substomatal chambers (Bowns 1973). Gibson (1996) state that more than 90% of non-succulent woody species in warm, inland deserts have amphistomatic leaves. However, hypostomatry has been observed in blackbrush shrubs, which are most common in semi-arid upland sites (Gibson 1996). Plants with hypostomatic desert leaves are probably not successful colonizers of warm desert habitats (Gibson 1996).

Anatomical Characteristics

Blackbrush leaves contain a double-layered (biseriate) epidermis (Table 2) that is small, dense, and flat. Blackbrush leaves have thick, well-developed waxy cuticle on leaf blades and thick epidermal cell walls (Table 2). The cuticle is thick in proportion to the leaf size, and is especially thick near the point of attachment of the epidermal hairs (Bowns 1973, Bowns and West 1976). Immediately beneath the biseriate epidermal cells, a relatively thick, highly vacuolated layer of uniseriate hypodermis is observed (Table 2). Hypodermis, having either collenchymas or sclerified cell walls, appears in blackbrush from relatively cool habitats, and is atypical of non-succulent warm desert plants (Gibson 1996). Although the precise function of hypodermis is not well understood, perhaps it is a mechanism to reduce transpiration and/or to resist tissue damage due to wilting and strong wind (Gibson 1996). A hypodermis occurs more often in tough sclerophyllous leaves; thinner, softer leaves generally do not have a hypodermis (Mauseth 1988). Bowns (1973) proposes that blackbrush leaf is made rigid and is supported by hypodermis (sub-epidermal collenchymas), which is especially well-developed near the adaxial surface. The presence of dense, uniseriate hypodermis may be largely contributed to the toughness and rigidity of blackbrush leaves, which in turn may endure extensive summer drought periods.

Below the hypodermis, the palisade parenchyma is readily distinguished from the spongy parenchyma (Table 2). The palisade parenchyma consists of multiple elongated (column-like) cells, mainly in the direction perpendicular to the leaf surface. Blackbrush leaves are bifacial. Palisade parenchyma of two- to three-layers thick (deep) occurs on the adaxial side only, and is filled with abundant chloroplasts. Gibson (1996) states that

Table 3. Geographic characteristics of southern Nevada blackbrush, southern California coastal chaparral, and warm, inland Mojave Desert Shrublands (From Horton and Kravel 1955, Hanes 1971, Barbour et al. 1987, and Gabler et al. 2005). An approximation of elevation, latitudinal, and longitudinal ranges is shown below.

Geographic Variables	Blackbrush	Mojave Desert	Chaparral
Elevational range (m)	1,160 to 1,830	Below 1,525	Below 1,830
Latitudinal range (N)	35°04′ to 41°15′	33°10′ to 38°21′	32°05′ to 35°06′
Longitudinal range (W)	114°01′ to 118°55′	113°30′ to 117°04′	116°17′ to 124°44′
Geographic zone	Inland	Inland	Coastal

typical desert leaves possess isolateral mesophyll, having at least some palisade parenchyma on the abaxial side or many palisade parenchyma layers throughout the transaction and frequently continuing around leaf margins. Multiple layers of palisade parenchyma occur in plants exposed to strong sunlight and the lower layers would receive enough light to photosynthesize effectively (Mauseth 1988).

The spongy parenchyma of blackbrush leaves is considerably less dense compared to palisade parenchyma, and contain rounded cells immediately beneath the palisade parenchyma, intermixed with some intercellular air space on the abaxial side of the blade (Lei 1999). Conversely, Mauseth (1988) states that in typical xerophytic plants, the spongy mesophyll may be lost altogether with only palisade parenchyma remaining, or there may be no intercellular spaces at all (Mauseth 1988). Such arrangement greatly reduces the ability to absorb carbon dioxide, but the benefit of water conservation apparently offsets this phenomenon (Mauseth 1988).

Relatively few shrubs species in warm, inland desert tend to have hypodermis, sunken stomata, and thickened epidermal cell walls (Gibson 1996). However, this statement is highly debatable because sunken stomata and thickened epidermal cells are also common adaptations in warm, inland desert plants. The sclerophyllous leaf design reveals an affinity of some southern Nevada plant species' morphology and anatomy with semi-arid coastal chaparral species as opposed to typical arid inland xerophytic plants, although sclerophyllous and xerophytic leaves share a number of common characteristics.

Plants from the Rosaceae family, including blackbrush generally do not occur in the most arid (dry) desert sites (Gibson 1996). Yet, the Rosaceae family is well represented in the cold desert of the Great Basin and in the chaparral vegetation of southern California (Mooney and Dunn 1970). In the southwestern United States, blackbrush shrubs occur in the transition zone between the cold desert and warm desert (Pendleton and Meyer 2004). Nevertheless, blackbrush shrubs do not occur in low Mojavean valleys of southern Nevada. The absence of blackbrush in the low Mojavean valleys is not strictly a function of elevation per se; perhaps many environmental attributes are associated with changing elevation.

Climatic and Geographic Attributes

Inland Mojave Desert shrublands and coastal Mediterranean chaparral shrublands share a number of geographic and climatic attributes in common (Tables 3 and 4, respectively). For instance, semi-arid Mediterranean climatic regions are found between 30 and 45 degrees north and south latitudes, on the west coasts of major continents, and in the Mediterranean Sea region (Barbour et al. 1987). Southern Nevada and southern California apparently lie within this latitudinal belt (Table 4). Both xerophytic and

Table 4. Climatic attributes of southern Nevada blackbrush, southern California chaparral, and warm Mojave Desert shrublands (From Horton and Kravel 1955, Hanes 1971, Bowns and West 1976, Barbour et al. 1987, Gabler et al. 2005, as well as Lei and Walker 1997).

Climatic variables	Blackbrush	Mojave Dessert	Chaparral
Air temperature			
Summer	Very high	Very high	High
Winter	Low	Mild	Low
Precipitation			
Summer	Very low	Very low	Very low
Winter	Low	Very low	Low
Sunny days	Many	Many	Many
Cloud cover	Very little	Very little	Little
Fog	Rare	Rare	Moderate
Relative humidity	Very low	Very low	Mild
Evaporation	Very high	Very high	Mild
Evapotranspiration	High	High	Moderate

sclerophyllous plants must endure prolonged summer droughts regardless of the amount and timing of winter precipitation (Miller et al., 1983). The arid continental desert of southern Nevada resembles the coastal Mediterranean-type climate characterized by cool winters with light precipitation and warm, dry summers in addition to long periods of sunny days and cloudless skies (Barbour et al. 1987, Munz 1974). The Mediterranean-type climate has more precipitation concentrated in cool winter months and summer drought annually, along with warm to hot summer and mild winter air temperatures (Table 4). In southern Nevada and California, rarely more than one inches of rainfalls occur during summer months (Specht 1968), with an exception of occasional major storm events. Typically, summer thunderstorms are episodic, short in duration, and may be so intense locally that most water will run off the soil surface before water infiltration process occurs (Barbour et al., 1987). Southern California has a year-round, marine-moderated atmosphere with coastal fogs, which are more frequent in spring and summer than in autumn and winter seasons (Hanes 1971). Nevertheless, southern Nevada is an arid continental desert due to the present of the Sierra Nevada in California intercepting moisture-laden Pacific winds, thus forming rainshadows and resulting in arid climate with warm desert landscapes.

Edaphic Attributes

Both inland Mojave Desert and coastal chaparral shrublands also share a number of edaphic attributes in common (Table 5). For instance, xerophytic and sclerophyllous plants often occur on gravelly/stony soils with little organic matter (Table 5, Barbour et al. 1987). Desert and chaparral soils generally have low water content and available nutrients (Table 5), including deficiencies in nitrogen, phosphorus, potassium, and sulfur (Specht 1968). By enduring the unfavorable and imbalanced chemical ratio of soil, extensive monospecific blackbrush and chaparral shrublands benefit from the near absence of competing woody perennial plants (Bakker 1984). Low soil moisture is largely associated with low annual precipitation. Desert and chaparral soils are relatively shallow with no distinct soil profiles (Table 5) due to the presence of hardpan (Specht 1968). Blackbrush shrublands containing dense monospecific blackbrush stands are frequently found at mid-elevations with relatively cool, semi-arid habitats in southern Nevada. The

Table 5. Edaphic attributes of southern Nevada blackbrush, southern California chaparral, and warm Mojave Desert shrublands (From Specht 1968, Hanes 1971, Bowns and West 1976, Barbour et al. 1987, Gabler et al. 2005, as well as Lei and Walker 1997).

Edaphic variables	Blackbrush	Mojave Dessert	Chaparral
pH	Slightly alkaline	Moderately alkaline	Slightly acidic
Moisture	Low	Very low	Low
Depth	Very shallow	Very shallow	Shallow
Organic content	Low	Very low	Low
Mineral nutrient	Very low	Very low	Very low
Surface	Stony/gravelly	Stony/gravelly	Stony/gravelly
Texture	Sandy	Sandy	Sandy-loam
Parent material	Limestone/domolite	Limestone/domolite	Igneous/metamorphic
Profile	Not distinct	Not distinct	Not distinct

sclerophyllous leaf design in blackbrush may also be associated with, or an adaptation to, arid habitats with infertile edaphic conditions and water deficiencies during arid summer seasons (Beadle 1966).

Conclusions

No consensus from currently literature has been reached to determine whether blackbrush is a xerophytes or a sclerophyll since blackbrush leaves possess a number of morphological and anatomical traits that are common in both woody xerophytes and sclerophylls. Such traits include semi-evergreen, thick blades and cuticle, abundant small leaves, tough leathery (rigid) leaves, hypostomatry, sunken stomata, thickened epidermal cell wall, as well as dense abaxial and adaxial pubescens. Additionally, blackbrush shrubs often exhibit summer dormancy, with characteristics of revolute margins, uniseriate hypodermis, biseriate epidermis, bifacial palisade parenchyma, and intercellular air spaces in leaves, which are sclerophyllous traits in leaves of chaparral plants.

The precise distinctions between xerophytes and sclerophylls are not conspicuous, presumably due to many similar environmental attributes between semi-arid coastal sclerophyllous chaparral and arid continental Mojave Desert shrublands. Nonetheless, this review article suggests that blackbrush are more similar to coastal chaparral plants in southern California than to low-elevation inland desert plants in southern Nevada from morphological and anatomical perspectives.

Literature Cited

Bakker, E.S. 1984. An island called California, 2nd edition. University of California Press, Berkeley, California.

Barbour, M.G. 1969. Age and space distribution of the desert shrub *Larrea divaricata*. Ecology, 50: 679–685.

Barbour, J.H. Burk and W.D. Pitts. 1987. Terrestrial plant ecology. The Benjamin/Cummings Publishing Company, Inc., Menlo Park, California.

Beadle. N.C.W. 1966. Soil phosphate and its role in molding the Australian flora and vegetation, with special reference to xeromorphy and sclerophylly. Ecology, 47:992–1007.

Bowns, J.E. 1973. An autecology study of blackbrush (*Coleogyne ramosissima* Torr.) in southwestern Utah. Doctoral dissertation. Utah State University, Logan, Utah.

——— and N.E. West. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southwestern Utah rangelands. Department of Range Science, Utah State University. Utah Agricultural Experimental Station, research report 27.

Gabler, R.E., J.F. Peterson, and L.M. Trapasso. 2005. Essentials of physical geography. Thomson Brooks/Cole, Pacific Grove, California.

Gibson, A.C. 1996. Structure-function relations of warm desert plants. Spring-Verlag, Berlin, Germany.

Hanes, T.L. 1971. Succession after fire in the chaparral of southern California. Ecological Monographs, 41:27–52.

Horton, J.S. and C.J. Kraebel. 1955. Development of vegetation after fire in the chamise chaparral of southern California. Ecology, 36:244–262.

Lei, S.A. 1999. Ecological leaf anatomy of seven xerophytic shrub species in southern Nevada. The 10th annual Wildland Shrub Symposium: Shrubland ecotones, Provo, Utah.

——— and L.R. Walker. 1997. Biotic and abiotic factors influencing the distribution of *Coleogyne* communities in southern Nevada. Great Basin Naturalist, 57:163–171.

Mauseth, J.D. 1988. Plant anatomy. The Benjamin/Cummings Publishing Company, Inc., Menlo Park, California.

Miller, P.C., D.K. Poole, and P.M. Miller. 1983. The influence of annual precipitation, topography, and vegetation cover on soil moisture and summer drought in southern California. Oecologia, 56: 385–391.

Mooney, H.A. and E.L. Dunn. 1970. Convergent evolution of Mediterranean-climate evergreen sclerophyll shrubs. Evolution, 24:292–303.

Munz, P.A. 1974. A flora of southern California. University of California Press, Berkeley, California.

Pendleton, B.K. and S.E. Meyer. 2004. Habitat-correlated variation in blackbrush (Coleogyne Ramosissima: Rosaceae) seed germination response. Journal of Arid Environments, 59:229–243.

Rowlands, P.G., H. Johnson, E. Ritter, and A. Endo. 1977. The Mojave Desert. In: M. Barbour and J. Major, eds. Terrestrial vegetation of California. John Wiley and Sons, New York, New York.

Rundel, P.W. and A.C. Gibson. 1996. Ecological communities and processes in a Mojave Desert Ecosystem: Rock Valley, Nevada. Cambridge University Press, Cambridge, Massachusetts.

Specht, R.L. 1968. A comparison of the sclerophyllous vegetation characteristics of Mediterranean-type climates in France, California, and southern Australia. Australian Journal of Botany, 17:277–292.